*Time, Morphology, and Neoteny in the Evolution of Man**

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> The primary function of a working hypothesis is to arrange facts into suggestive patterns capable of guiding observations and experience into meaningful channels.
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> —Th. Dobzhansky (1950:399)

INTRODUCTION

WITH the recent removal of three modernlike forms of man as claimants to an extreme antiquity, namely, Galley Hill (Oakley and Montagu 1949; Montagu and Oakley 1949), Bury St. Edmunds (Baden-Powell and Oakley 1952), and Piltdown (Weiner, Oakley and Le Gros Clark 1953), the theory held by some anthropologists that modernlike types of man appeared quite early in the evolution of the genus (Leakey 1934, 1953; Montagu 1951a, b; Vallois 1952; Teilhard de Chardin 1953) has been somewhat shaken.

Galley Hill and Bury St. Edmunds are relatively recent forms, and the Piltdown cranial remains have now been finally declared fraudulent, being subfossil and post-Pleistocene (Oakley 1954c).

There remain a number of other fossil human forms, some of undoubted antiquity and some of disputed antiquity, for which a morphological status similar to that of modern man has been claimed. It is desirable that the facts concerning these modernlike fossil forms be clearly restated. Since the available evidence indicates that these modernlike forms evolved prior to the neanderthaloids and were contemporary (in time if not always in locality) with pithecanthropoids, it is difficult for many of us to understand from what ancestors and by what means such modernlike forms could have evolved. In the present paper I shall attempt to indicate a means by which this perplexity may be relieved.

It should be at once stated that I hold no special brief for the theory of the antiquity of morphologically modern forms of man. I am principally concerned to evaluate the significance of certain facts which at the present time appear to be incontrovertible. These incontrovertible facts are the morphologically modern types of man that existed in times prior to the appearance of neanderthaloid forms of man. The problem upon which we shall attempt to throw some light in this paper is the means by which such modernlike forms of man came into being so early in the evolutionary history of man. The theory to be proposed can at best be envisaged as a suggested solution of a problem—a problem which may, with the advance of knowledge, turn out to be a perfectly spurious one—spurious if the datings and/or the morphology of certain of the fossil forms discussed in the body of this paper prove not to be what they at the present time appear to be. That this is a very real possibility no one who is acquainted with the recent history of human paleontology can have the least doubt. Certainty in these matters is a question of the degree of probability which attaches to the judgment of authorities that their statements are sound. As I write these words the ghost of the Piltdown hoaxer rubbing his hands together with invisible soap smiles down mischievously at us. It is devoutly to be hoped that his cautionary presence will long continue to haunt our deliberations.

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* I am most grateful to Sir Gavin R. de Beer, Director of the British Museum (Natural History), for his helpful reading of this paper.

TIME AND MORPHOLOGY

In the classical version of man's evolution, time and morphology maintain a one-to-one association in a simple concomitant relation. This relation has usually been conceived in the form: the longer the elapsed time, the more advanced the morphological development. Such a relationship was implicit in the theory of evolution, in the conception of the progressive evolution of complex from simpler forms.

During the nineteenth century paleontologists provided several impressive demonstrations of the apparent soundness of the time-morphology relationship. Among the most notable of these was the reconstruction, by Marsh and Cope some seventy years ago, of the horse family tree from the Eocene to the present time. The remarkable transformation of Eocene eohippus (*Hyracotherium*) to recent *Equus* could actually be seen in the models and charts which were so widely circulated. One could travel, as it were, in a straight line beginning some sixty million years ago with eohippus and emerge into the present firmly seated on the back of *Equus*. The mulishness with which this view has been maintained would suggest that the species involved was the ass (*Equus asinus*). At any rate, the rectilinear view of the evolutionary process which such reconstructions conditioned exercised a considerable influence upon the thought of contemporary biologists and helped to establish the concept of orthogenesis (Haacke 1893; Eimer 1898), that is to say, "straight origin" or "straight line" evolution. Such reasoning now seems to us somewhat like a steeplechased conclusion, and perhaps indicates the equine tendency of the human mind to jump to conclusions without properly taking the obstacles or, as one paleontologist has wryly remarked, to put the chart before the horse. Needless to say, such charts were drawn up for numerous other animal groups including man. Indeed such orthogenetic charts purporting to illustrate the evolution of man are still to be found in some contemporary works.

THE CONCEPT OF ORTHOGENESIS

The concept of orthogenesis has been effectively dealt with by Jepson (1949), and more recently by Simpson (1953). It will not be far wrong to say that orthogenesis is now generally considered to be an unsound idea, one that puts the evolutionary process into a strait jacket which deforms the realities of that process, a process which is more accurately conceived as a multidimensional reticulum. It would, however, be incorrect to suggest that the concept of orthogenesis is a "dead horse," and that any comment on it is to be conceived as an attempt at resuscitation for the purpose of an utterly superfluous flogging. The fact is that there are still some paleontologists and paleoanthropologists whose thinking seems even now to be dominated by an orthogenetic conception of man's evolution.

The concept of orthogenesis came into its own at about the time when some of the most important discoveries relating to the prehistory of man were being made. The tools of prehistoric man had already been shown to follow the evolutionary principle in the succession from the simple to the more complex in what, again, was assumed to follow a rectilinear progression. By the 1870's, C. J. Thomsen's system of the three ages—the Stone Age, the Bronze Age, and the Iron Age—had been generally accepted (Daniel 1943). Progression in time from the simple to the complex could not be more clear (Childe 1953). With the discovery of *Pithecanthropus erectus* in Java in 1891, and the extraordinary number of Neanderthal types that were found in Europe during the first decade of the twentieth century, followed by the discovery of prehistoric types resembling modern man, such as those of Cro-Magnon, Grimaldi, and Předmost, the straight-line morphologic evolution of man seemed to be equally clear—from ape-man *Pithecanthropus* through intermediate Neanderthal man, to modern man. Time and morphology appeared to fit perfectly in the expected linear progression: the more primitive, that is, the more ape-like the morphology, the earlier in time did the group exhibiting that more primitive morphology appear; the more "advanced" the morphology, the later in time did the group exhibiting it appear. This view has been most recently defended by Washburn (1954:438). As an expression of a general relationship this statement may be unexceptionable, but as a statement calculated to embrace all cases, it is open to considerable question, and it is possible that it has somewhat tended to obscure the actual history of hominid evolution.

The linear conception of man's evolution seemed reasonably satisfactory—except for the strange case of the apparently ancient Galley Hill skeleton—until the discovery in 1935 and 1936 of the occiput and left parietal bone of Swanscombe man in an undoubted Middle Pleistocene Second Interglacial deposit (in Kent, England). The bones were associated with an Early Middle Acheulean type of industry which served to corroborate their geological antiquity. Chemical tests have further served to confirm the geological findings. The remarkable thing about the Swanscombe bones is that, except for their thickness, they might in every way have been those of a modern female (Le Gros Clark 1949:94). Zeuner's application of the Milankovitch curve yields an age of about 250,000 years for Swanscombe (Zeuner 1952); Oakley (1953:45) would conservatively prefer to say, "More than 100,000 years." The important fact is that Swanscombe appears to be a morphologically more modernlike type than types of man such as the neanderthaloids, that do not seem to have appeared until much later. Swanscombe belongs to the Second (Mindel-Riss or Great) Interglacial, whereas the earliest neanderthaloid, the Steinheim skull, belongs either to the Late Third Glacial (Riss) or the Third Interglacial

(Riss-Würm). It is of interest to note that the human occipital bone recovered from a cave near Quinzano in the commune of Verona in 1938 closely resembles the Swanscombe occipital, and is referred to the early Middle Paleolithic level of the cave "corrispondente, con tutta probabilità, all'interglaciale riss-würmiano, senza escludere per i livelli piu profondi della cava un'eta ancora più antica" (Battaglia 1948:20). The neanderthaloids Ehringsdorf, Galilee, Mount Carmel, Saccopastore, are from the Third Interglacial, while La-Chapelle-aux-Saints, La Ferrassie, La Quina, Monte Circeo, and probably Le Moustier, are Fourth Glacial (Würm I).

The neanderthaloids are by no means a homogeneous group, as has usually been assumed but, as Howell has pointed out, the early neanderthaloids differ from the later classic Neanderthals in many morphological respects. According to Howell (1951), in the Riss-Würm early Neanderthals the skull was slightly shorter, narrower, and higher than in the later classic Würm I Neanderthals, the supraorbital tori were slightly heavier, the parietals were slightly more expanded, the vault more arched, and the occipitals more expanded, the cranial base is more flexed, the external auditory meatus tends to be vertically elliptic rather than horizontally so, and the tympanic plate tends to be vertically or obliquely oriented, the facial skeleton tends to be smaller, there is a tendency to separation of ciliary and orbital portions of the supraorbital torus, the malar is large with sharp demarcation between it and maxilla, and there is a tendency to formation of a canine fossa.

In most of these traits the early Neanderthals more closely resemble modern man than do the later Neanderthals.

THE SIGNIFICANCE OF FONTÉCHEVADE

Another form of fossil man preceding the neanderthaloids is Fontéchevade. Fontéchevade is known from *two* specimens from the Third Interglacial, associated with a Tayacian industry which antedates the industries known to be associated with the Neanderthals. Fontéchevade man (from the cave near the village of Montbrun, Department of Charente, France) would appear to be in almost all respects a modern type of man (Vallois 1949, 1952; Montagu 1951b). The Piltdown cranial bones were thought to be of about the same age as Fontéchevade, namely, some 50,000 years (Oakley 1953), but are now known to be post-Pleistocene (Oakley 1954c). Except for thickness, the Piltdown cranial bones constitute those of a modernlike form of man.

Howell, who, to judge from a recent paper (1952), is not an orthogenist, nevertheless in an earlier paper (1951) comes very near fitting all these forms of men into an orthogenetic scheme. Thus, he sees the evolution of prehistoric hominid forms passing from Second Glacial (Mindel) Heidelberg man to Second Interglacial (Mindel-Riss) Swanscombe man (whom Howell regards as a neanderthaloid form), through Steinheim, to the Neanderthals, and finally to Homo sapiens. It may well be that this view will ultimately prove correct; at the present time, however, I think it disregards as well as misinterprets some rather important evidence. For example, Howell states that "the characters of Fontéchevade differ little from those of the early Neanderthals," that "the Fontéchevade skull is tentatively regarded as another possible representative of the early Neanderthal group" (1951:409, 412). Vallois (1949:348), who originally described the Fontéchevade remains, unequivocally states that they are not in any way neanderthaloid. Concerning Fontéchevade II (the more complete skull) Vallois writes, "Reconstruction of the frontal . . . therefore confirms this important fact: he had a forehead constructed on the same type as our own, and totally devoid of the torus so characteristic of the Neanderthals." With respect to Fontéchevade I Vallois writes, "The essential fact is the absolute absence of a supraorbital torus: the glabella and brow ridge are less developed than in the Upper Paleolithic Europeans, or even the majority of Europeans today" (1949:352). Having examined the original bones through the courtesy of Professor Vallois, I can in every way confirm these statements (Montagu 1951b). Fontéchevade I is represented by a beautifully preserved fragment of the critically important glabellar and orbital margin region, in what was probably an adult or possibly late adolescent female, and there can be not the least question of the accuracy of Vallois' description of it.

The fact is that Fontéchevade is both temporally and culturally of earlier age than the early and classic Neanderthals (with the possible exception of Ehringsdorf). One cannot deal with Fontéchevade by turning that type into what it is not—namely, a Neanderthal form. Nor is there any morphological ground for treating Swanscombe in a similar manner. Overlooking the striking modernity of Fontéchevade I by overlooking that specimen altogether will not serve to advance our thinking in these matters. If our theories are going to make us insensible to the facts, it were better that we looked again at the facts and re-examined our theories in the light of them.

Since Washburn (1953:761) has asserted that "Neither the back of Swanscombe nor the top of Fontéchevade permit the reconstruction of the face," it requires to be pointed out that part of the "top" of Swanscombe is available in the form of the left parietal, and that with respect to Fontéchevade I, as Vallois and I have independently stated, sufficient of the bone is present to enable us to reconstruct the facial skeleton—a facial skeleton which would almost certainly resemble that of a modern European. Concerning Fontéchevade II there might have been a reasonable doubt. Concerning Fontéchevade I there can be none.

In the two Fontéchevade specimens we have back, top, sides, and the critical fronto-orbito-nasal region. The latter resembles the same region in a modern European, except that, as Vallois has pointed out, it is even more delicately made than in the average European female skull of today. It may well be asked whether anyone has ever seen a modernlike adult or late adolescent fronto-orbito-nasal region with a facial skeleton that was not of a modern variety? It is greatly to be regretted that neither photographs, drawings, casts, or even a thorough description of Fontéchevade I have thus far been made available. Had any of these things been done there could be little doubt in anyone's mind concerning the morphological status of Fontéchevade.

KANAM, KANJERA, AND SWANSCOMBE

In the field of paleoanthropology there are many facts but much uncertainty. For example, there is the Kanam jaw from East Africa (Leakey 1934). This is of modern form, and is thought to be by its discoverer, L. S. B. Leakey—and by others—of Lower Pleistocene age. Unfortunately the original site at Kanam has been washed away, and owing to the heavy fluorinization of the soil fluorine values are useless, and there appear to be no means at the present time by which the actual age of this fossil jaw can be determined. For the purposes of the present discussion we shall suppose that the Kanam jaw is of Lower Pleistocene age—what then? How could the early occurrence of such a modern type be explained?

The fragments of the three Kanjera skulls found by Leakey in a datable deposit of later Middle Pleistocene age, "roughly contemporary with the Swanscombe beds" (Leakey 1953:204), except for their thickness are modernlike in form. As at Swanscombe, the Kanjera skulls were found in beds containing tools of Acheulean industry.

Let us suppose that Swanscombe and Kanjera are modernlike types, except for greater thickness of cranial bones (in the areas of greatest difference it is doubtful whether the thickest-boned prehistoric skull ever exceeds its modern counterpart by as much as 3 mm.). That Fontéchevade I is of modern type there can be little doubt. How are we to explain the morphology of these types in relation to other morphologically different but related types, and in relation to the temporal levels at which they supposedly occur?

It is usually assumed that the neanthropic cranial type represents the latest cranial form to be evolved, and that the Neanderthal cranial types represent earlier more primitive forms. May it not be, however, that the reverse is the case? That the neanthropic cranial type actually represents a much less specialized, really more primitive, type than the Neanderthal? Indeed, we have already seen that in many traits of the skull the early Neanderthals are themselves more like neanthropic men than are the later Neanderthals. If hominid fossils such as Kanam, Swanscombe, and Kanjera are eventually shown to be, the one of Lower Pleistocene age and the others characterized by a neanthropic fronto-facial morphology, this suggestion will be strengthened and we shall have to seek for an anthropoid-ape group which will possess the necessary unspecialized qualifications for a hominid ancestor. In the case of Swanscombe the facial bones are missing, but in Kanjera 3 the form of the frontal region is the same as in modern man, and a portion of the maxilla shows that the canine fossa must have been of modern type (Leakey 1934:208).

THE POSSIBLE ANCESTORS OF HOMO SAPIENS

Except for the fact that we do not know their exact geological age the fossil australopithecines of South Africa, and especially the form described as *Telanthropus* (Robinson 1953), seem to be the group of manlike apes making the closest approach to the postulated unspecialized anthropoid–ape-like ancestors of man. Let us assume that the Australopithecinae are directly ancestral to the Hominidae. The Australopithecinae in fact may or may not represent the actual group of manlike apes from which man is descended. The morphological indications are that man is directly descended from a more manlike group of primates and that the australopithecines are a closely related annectant of this latter group. Cultural evidence for the existence of such a more advanced group is found in South Africa in the form of a pebble-tool culture (Oakley 1954a, b). The australopithecine group, however, so closely resembles what we would expect the group ancestral to the Hominidae to be like, that for our practical purposes we may assume it to have been the australopithecine group.

Homo, then, is to be conceived as having evolved from an erectly walking bipedal ape with a large proportion of the characters of the ape skull, except that the deciduous teeth, at least, were more manlike than apelike, while the brain ranged in size from that of a great ape to a size attained by very small human brains but never achieved by any other known primates. Broom and Robinson (1952) estimated the cranial capacity of the larger members of the fossil group he named *Paranthropus crassidens* to be well over 900 cm^3—the average capacity being about 750 cm^3 (Robinson 1953:497). Robinson (p. 498) has estimated that *Telanthropus capensis* had a cranial capacity of between 850 and 950 cm^3. This estimate may possibly err on the generous side. The maximum cranial capacity recorded for an anthropoid ape was 685 cm^3 in an adult gorilla (Hooton 1942:88), the minimum brain weight recorded for a human being of apparently normal intelligence was 788 grams or about 830 cm^3 (Hechst 1932; Le Gros Clark 1948). If Robinson's lower estimate is correct then the brain of *Telanthropus* falls within the lower limits of the range for human brain size. But even if Robinson's lower figure is an overestimate it probably does not err by much and puts *Telanthropus* in respect of brain size close to the hominid line. The cranial capacity of *Pithecanthropus robustus* was about 900 cm^3.

The hominid form most resembling the australopithecines is *Pithecanthropus robustus* from the Lower Pleistocene of Java (Lower Pleistocene *Meganthropus palaeojavanicus* and *Gigantopithecus blacki* are considered by some authorities [Broom 1946:138] to be giant australopithecines). Middle Pleistocene *Pithecanthropus erectus* of Java, and *Sinanthropus pekinensis* of the same age from China, follow next in morphological resemblance—which is not necessarily morphological or temporal order. Next follows the Upper Pleistocene Java Solo man (Weidenreich 1951). Solo man belongs either to the end of the Third Interglacial or the beginning of the Fourth Glacial. This pithecanthropoid type is undoubtedly a descendant of the older pithecanthropines, and the persistence of Solo man possibly into the Fourth Glacial (Von Koenigswald 1951:221) affords us an opportunity to study the evolution of a hominid group in what seems to have been a thorough geographic isolation from other hominid groups. We may thus observe the trend of evolution from *Pithecanthropus robustus* through *Pithecanthropus erectus* to Solo man. The changes over this great period of time, which we may conservatively put at 500,000 years, are both absolutely and relatively minor—but changes there have been. These changes we know to have affected the brain, in the filling out of the antero-inferior parieto-temporal region (Weidenreich 1947:180), while in the skull the structure of the foramen magnum is unique in that its anterior half faces more or less downwards whereas the posterior half faces backwards (Weidenreich 1951:259). There are other interesting but minor changes. The important fact is that in Solo man we have an insular terminal hominid type which is morphologically clearly descended and but little altered from *Pithecanthropus robustus*. In other words, the rate of evolutionary change in the geographically isolated group of Javanese pithecanthropines was comparatively slow compared with that which appears to have been occurring in other hominid groups elsewhere. It is possible that in Solo man we have an example, in miniscule, of what Simpson (1953:319) has called bradytely, that is, lack of appreciable evolutionary change over a long period of time.

If, as is generally done, we assume a monophyletic origin for man in the Early Pleistocene or Late Pliocene, it should be abundantly clear that to account for such different contemporary morphological types as Solo and Fontéchevade man (each from the latter part of the Third Interglacial) and such earlier differing contemporaneous (Middle Pleistocene) types as, on the one hand *Pithecanthropus erectus*, and Kanjera and Swanscombe man on the other, it will be necessary to consider every evolutionary process which may possibly have played a role in producing such types.

EVOLUTIONARY RATES

Starting as members of a common morphologically similar phyletic group, separated or isolated populations could, as the result of differences in rates of evolution, become significantly differentiated from one another, and this even though the trend or direction of evolution may remain the same. In this manner it would be possible to account for certain phenomena in the evolution of man which upon a naïve or orthogenetic view appear to be irreconcilable.

For our purposes an evolutionary rate may be defined as a measure of morphological change relative to a given period of elapsed time. Simpson (1953) has recently fully discussed the varieties of evolutionary rates, and for a discussion of this subject the reader may be referred to his work. It is now fairly well understood that there has been the widest possible variation in evolutionary rates in the evolution of living forms. Simpson tells us, for example, that, "Of North American mammalian stocks introduced into South America in latest Pliocene and/or early Pleistocene, that is, perhaps from a million to 500 thousand years ago, probably all have become specifically distinct, many have become generically distinct, but none has become so distinct as to be reasonably placed in a new subfamily or family." And Simpson adds that, as he had already noted earlier in his book of other single examples, "this represents an increased average rate of evolution accompanying occupation of new territory" (1953:37). The evolutionary rates of the members of the same groups which remained in North America changed in an appreciable but somewhat lesser degree.

Occupation of new territory, to judge from the wide distribution of fossil man upon the earth, and the wanderings of peoples (Haddon 1911; Febvre 1925; Taylor 1937), appears to have been a not infrequent activity of many prehistoric human populations. Such prehistoric populations seem to have been very small (Krzywicki 1934), so that genetic changes could have become rapidly established in them (Montagu 1950).

As Simpson has pointed out (1953:78), man as a mammal must be considered to have evolved at a more than average rate, and as a mammal of quite ordinary inherent variability he owes his present great intergroup variation to the fact that he has adapted to a uniquely large number of different habitats—the habitats of man being not merely the differing physiographic environments but including also the different sociocultural environments (Dobzhansky and Montagu 1947; Tappen 1953; Montagu 1954).

PEDOMORPHOSIS, FETALIZATION, NEOTENY

Mutations have, of course, occurred—and occur—in the members of all human populations, but in accounting for evolutionary differences in man it seems unnecessary to assume substantially different mutation rates in different separated early groups of man to account for the contemporaneity of palanthropic and neanthropic types. It is here that the process of pedomorphosis (Garstang 1922) may play a significant role. The original notion of paedogenesis, as he called it, was elaborated by Von Baer in 1828, to describe the development of mature germ cells in a larval body. The concept of neoteny was quite clearly discussed by T. E. V. Boas in 1896 as the process by which the young features of the ancestor are retained in the adult stage of the descendant. The concepts of fetalization, as proposed by Bolk (1926, 1929), and neoteny, by De Beer (1930, 1932, 1938, 1939, 1948, 1951), proterogenesis by Schindewolf (1950), and bradygenesis by Ivanow (1945), mean pretty much the same thing as paedogenesis or pedomorphosis, except that, strictly speaking, fetalization would refer specifically to fetal stages, while pedomorphosis would refer to young stages. Since the term "neoteny" embraces both these stages as well as the processes of rate implied in Schindewolf's and Ivanow's terms, it is to be preferred as the more comprehensive term.

It is reasonably clear that what is inherited by the organism has in part been acquired as a consequence of interaction of genotype with environment during development. It is during the process of individual development that mutations acquire phenotypic expression. Any mutation which serves to produce a relative retardation of somatic development so that the descendant fails to pass through several of the developmental stages of the ancestor, will result in the descendant exhibiting a pattern of growth which in the adult stage represents a retention of the ancestral fetal or youthful pattern. Many such cases are known to zoologists and geneticists (Garstang 1922; Bystrow 1938; Romer 1942; De Beer 1951), in which rates of development, the retention of an embryonic or youthful character and its extension in the adult, duration of developmental periods, and termination of development are affected by mutations which may have distinct and marked effects upon adult form. Such neotenous mutations may spread rapidly in a small population, and it is suggested that under such conditions the fetal or juvenile developmental stage of a pithecanthropine or similar type could have become very quickly consolidated in the descendant group. A fetalized pithecanthropine, to judge from the juvenile Modjokerto skull, or a fetalized australopithecine, to judge from the juvenile *Australopithecus africanus*, would more closely resemble modern man than these fossil juvenile forms would the adult members of their own type. Spuhler (1954) has shown that the deciduous teeth of the australopithecines are more like the deciduous teeth of modern man, but the permanent teeth are more like those of apes. In almost all the traits in which the juvenile members of these fossil forms differ from the living apes and their own adult forms they most closely resemble modern man, for example, in the comparatively globular form of the skull, the thinness of the skull bones, the absence of brow ridges, the absence of crests, the form of the teeth, and the relative size and form of the brain. We can have little doubt as to the form and characters of the fetal forms of the australopithecine and pithecanthropine types—these would almost certainly more closely resemble the human than the anthropoid. It is by the retention of such fetal and juvenile characters in the adult, particularly in the head region, by neoteny, that a neanthropic type of man could have evolved quite early in the history of the human species. Drennan (1931:209) and Buxton and De Beer (1932) independently suggested that modern man may not be unrelated to a neanderthaloid type if he can be regarded as descended by neoteny from a juvenile form of the latter. But more recently De Beer (1951:57–58) has stated, "It is now realized that the ancestor of modern man could not have been Neanderthal man because he appeared later in time than the earliest types of modern man. But if the human ancestor was similar to *Pithecanthropus*, or *Australopithecus*, modern man would have descended from them by retention of features in the juvenile forms of their skulls, which is what is meant by neoteny."

Drennan (1937a:59) and, more recently, Abbie (1952:70) have argued that anthropologists have paid insufficient attention to the developing organism and too much attention to the adult form in the study of man's physical evolution. This, of course, has in large part been unavoidable, since most of the fossil remains recovered have been those of adults. Drennan feels that the gerontomorphic principle has been overstressed by anthropologists "by their interest in the classical examples of its expression in Java, Pekin, Neanderthal, and Rhodesian Man, etc., to the great neglect of the much more humanizing principle of pedomorphism which had to precede it" (personal communication, Jan. 21, 1954). Similarly, Abbie (1952:70) asserts "that the present method of trying to trace human evolution by comparison of adult forms is futile. The only common stem that can be found for the primates lies in an early embryonic series. In this series a sufficiently generalized precursor for man could be produced by practically any of the primates. Consequently, it is unnecessary to go very far back into primate history to find the ancestral form."

No one disputes neoteny as a factor of evolution in many lower animal groups. The questions for us to decide, in the light of the evidence, are whether it is at all probable that neoteny has occurred (1) as *a* factor in the evolution of man, and (2) as a factor in the early differentiation of man.

The suggestion of the present paper is that types such as Kanam, Kanjera, Swanscombe, Quinzano, and Fontéchevade constitute possible examples of forms of men in which evolution by neoteny may have played an appreciable role. Neotenous mutations may have occurred with different, but probably insubstantial, frequencies in different early hominid populations derived from a common stock, and hence, by this means, in isolated hominid populations, very appreciable morphologic changes could have been brought about. The selective advantages of such possible neotenous changes, as Dobzhansky (1950:399) has pointed out, is a subject which has received insufficient attention. What was the advantage of thick skull bones, if any, in palanthropic types? What is the advantage of thinner skull bones in neanthropic types? What were the advantages of supraorbital tori in the pithecanthropines and neanderthaloids? What is the advantage of the absence of these tori in neanthropic types? We don't know; we don't even have good theories. We need to think more about these matters much in the manner in which Coon, Garn and Birdsell (1950) have, with respect to the differences characterizing modern varieties of man. Above all, we need to investigate such matters by experimental means.

TIME AS A FACTOR IN EVOLUTION

In conclusion, a few words may be added on the dimension of secular time as a factor of evolution. Secular time is the matrix in which evolutionary change occurs. It is a universal constant, but time has no direct control upon evolutionary change. Time provides the constant against which change may be measured. Whatever it is that undergoes change is, however, developmentally influenced by time—change occurring as the result of the interaction of events which occur within time.

Time heals all wounds not because of its passage, but because of the occurrence of events during the passage of time which produce the healing. Were it not for those events no amount of time would be sufficient to produce the healing. Similarly, it should be clear that unless certain events occur no amount of time will serve to produce evolutionary change. However, time being the succession of instants during which events occur, time is obviously necessary for events to occur in. Time is, therefore, a factor or condition of evolution. Evolution needs time.

CONCLUSION

What we have been attempting to say in the present paper is that during the same length of secular time, rates of evolutionary change may vary appreciably in isolated populations of the same species. In man, with his somewhat unique breeding habits, and large differences in mobility—some early populations having been confined to a restricted habitat while others wandered over large continental areas, man having reached practically every part of the habitable globe—the possibilities of idiosyncratic variation have been greatly multiplied. Rates of evolutionary change in different early hominid groups during the same length of secular time, exhibited principally as differences in the rate of neotenous mutations—among other factors—are quite sufficient, it is suggested, to explain such apparent anachronisms as neanthropic types of man in the Middle or even Early Pleistocene and a palanthropic type of man in the Upper Pleistocene—always, providing, of course, that we are also finally able to understand the adaptive value of these neotenous changes.

SUMMARY

The hypothesis advanced in this paper suggests that commencing with a single hominid ancestral population, which has subsequently separated into several geographically isolated populations, that in addition to such factors as mutation, natural selection, isolation, drift, and the like, neotenous mutations have played an important role in adding to the quanta of morphological difference among such populations. Neotenous mutations occurring at a more rapid rate in some early populations than in others would, at least in part, be responsible for the development of morphologically modernlike types of man at a period contemporary with the flourishing of such types as Pithecanthropus, Heidelberg, and Solo man. The hypothesis suggests that in the latter types neotenous mutations occurred comparatively infrequently.

REFERENCES CITED

ABBIE, A. A.
1952 A new approach to the problem of human evolution. Transactions of the Royal Society of South Australia 75:70–88.

ASHTON, E. H.
1950 The endocranial capacities of the Australopithecinae. Proceedings of the Zoological Society of London 120:715-21.

BADEN-POWELL, D. F. W. and K. P. OAKLEY
1952 Report on the re-investigation of the Westley (Bury St. Edmunds) skull site. Proceedings of the Prehistoric Society (London), Paper No. 1:1–20.

BAER, K. VON
1828 Ueber Entwicklungsgeschichte der Thiere. Beobachtung und Reflexion. Königsberg.

BATTAGLIA, R.
1945/48 Osso Occipitale Umano Rinvenuto nel Giacimento Pleistocenico di Quinzano nel Comune di Verona. Palaeontographia Italica 42, No. 2:1–31.

BOAS, J. E. V.
1896 Ueber Neotenie. Festschrift für C. Gegenbaur 2:1. Leipzig.

BOLK, L.
1926 Das Problem der Menschwerdung. Jena, Fischer.
1929 Origin of racial characteristics in man. American Journal of Physical Anthropology 13:1–28.

BROOM, R.
1946 The South African fossil ape-men: the Australopithecinae. Pretoria, Transvaal Museum.

Broom, R. and J. T. Robinson

1952 Swartkrans ape-man: Paranthropus crassidens. Pretoria, Transvaal Museum.

Buxton, L. H. D. and G. R. de Beer

1932 Neanderthal and modern man. Nature 129:940.

Bystrow, A. P.

1938 Dvinosaurus als Neotenische Form der Stegocephalen. Acta Zoologica19:204–95.

Childe, V. G.

1953 The constitution of archaeology as a science. *In:* Science, Medicine and History, ed. E. A. Underwood, Vol. I, pp. 2–15. London and New York, Oxford University Press.

Coon, C. S., S. M. Garn and J. S. Birdsell

1950 Races. Springfield, Ill., Thomas.

Cuenot, L.

1941 Invention et Finalité en Biologie. Paris, Doin.

1945 L'Homme ce Néoténique. Bulletin de L'Academie Royale Belgique (Brussels) 31.

1951 L'Evolution Biologique. Paris, Masson.

Daniel, G. E.

1943 The three ages: an essay on archaeological method. London and New York, Cambridge University Press.

De Beer, G. R.

1930 Embryology and evolution. London and New York, Oxford University Press. Also 1932, 1938, 1939, 1951.

1940 Embryology and ancestors. London and New York, Oxford University Press. Rev. ed., 1951.

1948 Embryology and the evolution of man. *In:* Robert Broom Commemorative Volume, pp. 181–90. Special Publication of the Royal Society of South Africa. Cape Town.

Dobzhansky, Th.

1950 Human diversity and adaptation. *In:* Cold Spring Harbor Symposia on Quantitative Biology XV: 385–400. Cold Spring Harbor, Long Island, N. Y., The Biological Laboratory.

Dobzhansky, Th. and M. F. Ashley Montagu

1947 Natural selection and the mental capacities of mankind. Science 105:587–90.

Ehrich, Robert W. and G. M. Henderson

1954 Concerning the Piltdown hoax and the rise of a new dogmatism. American Anthropologist 56, No. 3: 433–35.

Eimer, Th.

1898 On orthogenesis and the impotence of natural selection in species formation. Translated by T. J. McCormack. Chicago, Open Court.

Drennan, M. R.

1931 Pedomorphism in the pre-Bushman skull. American Journal of Physical Anthropology 16:203–10.

1937a A short course on physical anthropology. Cape Town, Mercantile Press.

1937b Human growth and differentiation. South African Journal of Science 33:64–91.

Febvre, L.

1925 A geographical introduction to history. New York, Barnes & Noble.

Frassetto, F.

1945/48 L'Occipital Fossile di Quinzano ed il Cranio di Londra Secondo una Moderna Metodologia. Palaeontographia Italica 42, No. 3:1–16.

Garstang, W.

1922 The theory of recapitulation. A critical restatement of the biogenetic law. Journal of the Linnaeus Society of London, Zoology 35:81.

Haddon, A. C.

1911 The wanderings of peoples. London and New York, Cambridge University Press.

HAACKE, W.
1893 Gestaltung und Vererbung. Leipzig, Weigel.

HECHST, B.
1932 Uber einen Fall von Mikroencephalie ohne Geistigen Defekt. Archiv für Psychologie 97.

HOOTON, EARNEST A.
1942 Man's poor relations. New York, Doubleday.

HOWELL, F. C.
1951 The place of Neanderthal man in human evolution. American Journal of Physical Anthropology, n.s. 9:121–54.
1952 Pleistocene glacial ecology and the evolution of "Classic Neandertal" man. Southwestern Journal of Anthropology 8:377–410.

IVANOW, A. N.
1945 A propos de la Phase Soi-Disant "Prophetique" dans l'Evolution des Kosmoceratidae. Bulletin de la Société Naturale Moscou, n.s. 50:31–32.

JEPSON, G. L.
1949 Selection, "orthogenesis" and the fossil record. Proceedings of the American Philosophical Society 93:479–500.

KOENIGSWALD, G. H. R. VON
1951 Morphology of Solo Man. American Museum of Natural History, Anthropological Papers 43:205–90.

KRZYWICKI, L.
1934 Primitive society and its vital statistics. London, Macmillan.

LEAKEY, L. S. B.
1934 Adam's ancestors. London, Methuen. 2nd ed., 1953.

LE GROS CLARK, W. E.
1948 Observations on certain rates of somatic evolution in the primates. *In:* Robert Broom Commemorative Volume, pp. 171–80. Special Publication of the Royal Society of South Africa. Cape Town.
1949 History of the primates. London, British Museum (Natural History).

MONTAGU, M. F. ASHLEY
1950 A consideration of the concept of race. *In:* Cold Spring Harbor Symposia on Quantitative Biology XV:315–36. Cold Spring Harbor, Long Island, N. Y., The Biological Laboratory.
1951a An introduction to physical anthropology. Springfield, Ill., Thomas.
1951b Neanderthal and the modern type of man. American Journal of Physical Anthropology, n.s. 9:1–3.
1954 Cultural and physical evolution. American Anthropologist 56:290.

MONTAGU, M. F. ASHLEY and K. P. OAKLEY
1949 The antiquity of Galley Hill man. American Journal of Physical Anthropology, n.s. 7:363–84.

OAKLEY, KENNETH P.
1953 Dating fossil human remains. *In:* Anthropology Today, by A. L. Kroeber and others, pp. 43–56. Chicago, University of Chicago Press.
1954a The dawn of man in South Africa. Royal Institution of Great Britain, Weekly Evening Lecture, 30 November 1954, 11.
1954b Dating of the Australopithecinae of South Africa. American Journal of Physical Anthropology, n.s. 12:9–23.
1954c The Piltdown bones and 'implements.' Nature 174:61–62.

OAKLEY, KENNETH P. and M. F. ASHLEY MONTAGU
1949 A reconsideration of the Galley Hill skeleton. Bulletin of the British Museum (Natural History) 1:25–48.

ROBINSON, J. T.
1953 Telanthropus and its phylogenetic significance. American Journal of Physical Anthropology, n.s. 11:445–501.

ROMER, A. S.
1942 Cartilage an embryonic adaptation. American Naturalist 76:394–404.
SCHINDEWOLF, O. H.
1950 Grundfragen der Paläontologie. Stuttgart, Schweitzerbart.
SIMPSON, G. G.
1953 The major features of evolution. New York, Columbia University Press.
SPHULER, J. N.
1954 Relationships of the Australopithecinae, the great apes, and man. Science News Letter 65:233.
STRAUS, W. L., JR.
1949 The riddle of man's ancestry. Quarterly Review of Biology 24:200–23.
TAPPEN, NEIL C.
1953 A mechanistic theory of human evolution. American Anthropologist 55:605–7.
TAYLOR, G.
1937 Environment, race and migration. Toronto, University of Toronto Press.
TEILHARD DE CHARDIN, PIERRE
1953 Sur la Probabilité d'un Bifurcation Précoce du Phylum Humain au Voisinage Immédiat de ses Origines. Comptes Rendus des Séances de l'Académie des Sciences 237:1932–53.
VALLOIS, HENRI V.
1949 The Fontéchevade fossil men. American Journal of Physical Anthropology, n.s. 7:339–62.
1952 Les Hommes fossiles. 4th ed. Paris, Masson.
WASHBURN, SHERWOOD L.
1953 The Piltdown hoax. American Anthropologist 55, No. 5, Pt. 1:759–62.
1954 An old theory is supported by new evidence and new methods. American Anthropologist 56:436–41.
WEIDENREICH, F.
1947 Some particulars of skull and brain of early hominids and their bearings on the problems of the relationship between man and anthropoids. American Journal of Physical Anthropology, n.s. 5:153–93.
1951 Morphology of Solo man. Anthropological Papers of the American Museum of Natural History 43:205–90. New York.
WEINER, J. S., KENNETH P. OAKLEY and W. E. LE GROS CLARK
1953 The solution of the Piltdown problem. Bulletin of the British Museum (Natural History) 2:141–46.
ZEUNER, F.
1952 Dating the past. 3rd ed. New York, Longmans.